FEEDING ECOLOGY AND MOVEMENT PATTERNS OF JUVENILE SABLEFISH IN COASTAL SOUTHEAST ALASKA

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A

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Abstract

Sablefish, *Anoplopoma fimbria*, is a commercially valuable groundfish species undergoing population declines in the Gulf of Alaska and Bering Sea. This study assessed the role of juvenile sablefish as consumers in coastal Southeast Alaska (St. John Baptist Bay, Baranof Island, Alaska; SJBB) to better understand their use of habitat and food resources during their early life history. Specifically, the diet of juvenile sablefish was described for multiple seasons (summer and fall) and years (2012 and 2013) from analysis of stomach contents recovered using gastric lavage. Sablefish ate a wide variety of prey taxa, and the most important prey groups were Pacific herring, smelts, and scavenged salmon remains. Diet differed between seasons and years, and scavenging of salmon carcasses occurred during fall sampling periods, revealing the ability of sablefish to capitalize on pulsed, high energy prey. We further explored habitat use by juvenile sablefish within SJBB by analyzing their vertical movement patterns using acoustic telemetry data. Sablefish that were frequently detected remained predominately near the bottom, but all fish remaining in range of the acoustic receivers made short excursions into shallower water. Generalized linear mixed models were used to determine the relationship between excursion frequency and daylight and tidal cycles. The excursion frequency was highest during slack and flood stages and at dawn and may be linked to foraging. Together, these findings suggest that juvenile sablefish may maximize their growth by accessing high energy pelagic and benthic prey while remaining on the bottom for the majority of time, potentially decreasing risk of predation.

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General Introduction

Sablefish, *Anoplopoma fimbria*, are one of the highest valued groundfish per pound in Alaska commercial fisheries (Sigler et al. 2001). Historically, sablefish were heavily exploited by foreign vessels, leading to a drastic population decline in the 1970s (Sigler & Lunsford 2001). Management actions and legislation reduced quotas and phased out the foreign fleet in the 1980s. By 1988, the sablefish fishery in Alaska was prosecuted completely by a U.S. domestic fleet. Alaska sablefish catches made by the domestic fleet in federal waters peaked at 38,406 t in 1988 and decreased to a catch of 12,280 t in 2013 (Hanselman et al. 2013). There has been a declining trend in sablefish biomass since the early 1990s; however, the stock is not considered overfished or nearing overfished levels (Hanselman et al. 2013). Instead, this decrease in biomass is thought to be partially due to poor recruitment, defined here as survival to reproductive maturity. Currently, there are state and federally managed longline and pot gear fisheries throughout Alaska.

Sablefish are distributed throughout the Pacific Ocean, from Mexico to the Bering Sea and from the Aleutian Islands westward to Japan (Mecklenburg et al. 2002). Sablefish found in Alaskan waters are considered a distinct population from those occurring further south, with some stock mixing off of the coast of British Columbia (Kimura et al. 1998). In Alaskan waters, sablefish experience a diverse range of environmental conditions throughout their lifespan, requiring different adaptations for successful growth, feeding, and reproduction (Sogard & Olla 1998, Sigler et al. 2001). Young-of-year (YOY) sablefish inhabit surface waters on or near the continental shelf and juveniles are often found in bays and inlets (Sigler et al. 2001). At maturity, sablefish migrate in a northwest direction from southeast Alaska to the Aleutian Islands and

Bering Sea, and migrate in the opposite direction at older ages (Maloney & Sigler 2008). Sablefish occupy greater depths with age and are demersal in slope waters and deep fjords as adults (Sigler et al. 2001, Maloney & Sigler 2008). Sablefish spawn in February at depths >300m (Mason et al. 1983), though specific spawning grounds have not been identified in the Gulf of Alaska or Bering Sea. Very little is understood about the early life stages of juvenile sablefish and the factors that affect successful recruitment.

In order to account for ecological interactions, such as predation and competition, in fishery management, it is necessary to identify food resources and habitat use of harvested species across multiple life stages (Latour et al. 2003, Duffy et al. 2010). The present study focuses on the juvenile life stage, when sablefish exhibit rapid growth rates (Rutecki & Varosi 1997, Sogard & Olla 2001) and there is potential for trophic interactions between sablefish and other species in coastal environments. Juvenile sablefish in bays and inlets may compete for limited space or food resources with salmon, forage fish, and many groundfish species. For example, Pacific herring, walleye pollock, Pacific Ocean perch and capelin show diet overlap with YOY sablefish (Yang & Nelson 2000) and could potentially compete with sablefish for shared resources. In addition, juvenile sablefish are vulnerable to predation, and have been found in the stomachs of adult coho salmon in Southeast Alaska (Rhea Ehresmann, Personal Communication 2014) and are found in the diets of piscivorous seabirds (Thayer & Sydeman 2007). Increasing our understanding of juvenile sablefish ecology provides opportunities to improve sablefish management by defining trophic interactions needed for ecosystem based management (Sigler et al. 2001, Latour et al. 2003).

The current study focuses on gaining a baseline understanding of juvenile sablefish ecology in Southeast Alaska. The study site was St. John Baptist Bay (SJBB), Baranof Island,

Alaska, where juvenile sablefish are known to be present during multiple seasons and years. In Chapter 1, juvenile sablefish diet was studied using nonlethal gastric lavage over five sampling periods in 2012 and 2013. The objectives of this chapter were to 1) quantify important prey resources used by juvenile sablefish, 2) describe seasonal and interannual variation in diet using multivariate techniques, and 3) identify ontogenetic shifts in diet. Chapter 2 used acoustic telemetry data collected by NOAA researchers in 2003 to monitor juvenile sablefish vertical movement. The objectives of this chapter were to 1) analyze depths used by juvenile sablefish and 2) describe the relationship between vertical movement and diel and tidal cycles. Generalized linear mixed models (GLMMs) were used to estimate the relationship between sablefish vertical movement and environmental factors.

Chapter 1:

Temporal variation in diet composition and use of pulsed resource subsidies by juvenile sablefish in coastal Southeast Alaska[1]

Abstract

Pulsed resources create an influx of energy that can provide individual and population level benefits to their consumers. As consumers, sablefish (*Anoplopoma fimbria*) experience strong seasonal pulses in prey resources during their period of juvenile growth in the nearshore marine environment. This study described temporal patterns in diet composition of sablefish (N=1,081) ranging in size from 226 mm to 455 mm FL during 4 sampling periods in summer and fall, 2012-2013, from St. John Baptist Bay, Alaska. Juvenile sablefish exploited a large variety of prey taxa characteristic of a generalist predator, with significant diet shifts among sampling periods revealing seasonal and interannual variation in resource use (ANOSIM; Global R=0.278, p<0.001). Diets were more diverse in 2012, when more invertebrate taxa were consumed, compared to 2013, when diets were dominated by Pacific herring and salmonid offal. In September of 2012 and 2013, spawning pink salmon (*Oncorhynchus gorbuscha*) were observed within the study area and juvenile sablefish capitalized on this high energy subsidy, with salmon carcasses among the top contributors to their diets by weight. However, sablefish also exploited lower energy in situ prey, such as benthic invertebrates, suggesting that they are not entirely reliant on seasonally pulsed, high energy prey. This study further emphasizes the significance of salmon as a vector of energy across ecosystems and is one of the first to

[1] Coutré, K.M. Beaudreau, A.H. and P. Malecha. 2014. Prepared for submission to Marine Ecology Progress Series.

document a marine teleost species scavenging on adult salmon carcasses in coastal marine waters.

Introduction

Access to high quality prey resources is essential for survival and growth of a consumer; however, these resources can be temporally dynamic (Hipfner 2008, Yang et al. 2008, Bentley et al. 2012). Many consumers exploit pulsed resources that create short-term influxes of energy within ecosystems (Yang et al. 2008, Yang et al. 2010, Bentley et al. 2012). Pulsed resource subsidies are low in frequency, diverse across systems, and variable within a system (Yang et al. 2010, Bentley et al. 2012). On the individual level, pulsed resources can increase the growth of the consumer (e.g. Wright et al. 2013) and potentially sustain the consumer during periods of low resource availability (Denton et al. 2009, Eberle and Stanford 2010, Yang et al. 2010). For example, Bentley et al. (2012) documented the profound impact that the influx of sockeye salmon (*Oncorhynchus nerka*) had by increasing ration size and growth rate of rainbow trout (*O. mykiss*) and arctic grayling (*Thymallus arcticus*) in two freshwater streams. Individual benefits from pulsed subsidies can also translate into population level effects for consumers. Large seed masting events by beech trees, *Nothofagus* spp., in New Zealand (occurring on 4-8 year cycles) have led to peak populations of mice feeding on these seeds, and increased survivability in stoats, a predator of the mice (King 1983). The population of consumer species often increases and can act as a lagged second subsidy pulse to other consumers in the system (Ostfeld & Keesing 2000). The magnitude and timing of pulsed subsidies may vary interannually, which has implications for predators that rely on them (Gende et al. 2002, Abraham & Sydeman 2004,

Yang et al. 2008). For example, in years of high salmon run size, bears (*Ursus* spp.) in Alaska selectively consumed the parts of salmon with the highest energetic value, while in years of low salmon returns, bears ate more whole fish (Gende et al. 2002).

At the population level, seasonal resource pulses can influence recruitment in marine fishes, though the extent of this influence is not well understood (Yang et al. 2008). The North Pacific Ocean has variable productivity, with a peak typically occurring in summer (Wong et al. 1995). Seasonal cycles of productivity can strongly influence forage fish and groundfish abundance within this region, with fish yields showing strong linkages to primary productivity and zooplankton abundances (Ware & Thomson 2005). For example, successful walleye pollock (*Gadus chalcogrammus)* recruitment is thought to be partially reliant on the pulse of copepods (*Calanus* spp.) during late summer and early fall in the Bering Sea (Coyle et al. 2011). In the nearshore marine environment, anadromous fishes such as Pacific salmon (*Oncorhynchus* spp.) and eulachon (*Thaleichthys pacificus*) provide a seasonal energy source for many predators (Sigler et al. 2004). In spring, Steller sea lions (*Eumetopias jubatus*) aggregate and forage on the energy-rich pre-spawning eulachon pulse in Berners Bay, Southeast Alaska (Sigler et al. 2004). Understanding the importance of periodic (e.g., seasonal) high energy prey to consumers can provide insight into ecological drivers of population variability.

Our study focuses on sablefish (*Anoplopoma fimbria*) as consumers in the nearshore marine environment of Southeast Alaska where there is strong seasonality and pulses in productivity. Sablefish are a demersal fish species in the northern Pacific Ocean that have shown highly variable year class strength (Sigler et al. 2001). Causes of this fluctuation are unknown; however, in the Gulf of Alaska strong sablefish year classes have been related to northerly drift in winter currents and warm temperature anomalies (Sigler et al. 2001). Age 0-2 sablefish inhabit

shallow waters on the continental shelf where they are active consumers (Cailliet et al. 1988, Rutecki & Varosi 1997, Sigler et al. 2001). In nearshore environments, juveniles experience a critical period of rapid growth (1.47 - 3.3 mm d^{-1}) before migrating to slope waters between ages 3 and 5 *(*Rutecki & Varosi 1997, Gao et al. 2004). Sablefish feed on zooplankton as larvae, and have been found to consume forage fish and invertebrates during the juvenile life stage in Monterey Bay (Cailliet et al. 1988, Sigler et al. 2001). In Alaska, sablefish diet information is limited and specific prey resources that contribute to their rapid growth in this region are unknown (Kendall & Clark 1985, Rutecki & Varosi 1997).

Across terrestrial and aquatic systems, the temporal scale at which a consumer population is studied impacts which food resources are identified as important (Ostfeld & Keesing 2000, Fortin 2002). Therefore, this study aims to identify important prey for juvenile sablefish in nearshore habitats on multiple temporal scales. Our first objective was to characterize the taxonomic diversity and body sizes of prey that juvenile sablefish consume. We hypothesized that juvenile sablefish diets would contain a variety of invertebrate and vertebrate prey characteristic of a generalist predator, such as euphausiids, cephalopods, and fish, based on previous studies (Cailliet et al. 1988, Yang & Nelson 2000). We expected that forage fish could be an important, seasonally-abundant prey resource, because juvenile sablefish in Monterey Bay have been found to prey heavily on Pacific anchovy (Cailliet et al. 1988). Our second objective was to quantify temporal variation in sablefish diet and describe their use of seasonal resource pulses. We hypothesized that diets would vary seasonally and between years. In other systems, juvenile fish have exhibited seasonal shifts in diet based on prey availability; for example, largemouth bass in Lake Opinicon, Ontario, shifted from a diet of zooplankton, insects, and small fish in July to predominantly zooplankton in September within the same year (Keast &

Eadie 1985). Sablefish may exploit seasonal pulses of productivity in the coastal marine environment, including anadromous fish that vary in timing and abundance across years. Our third objective was to identify ontogenetic shifts in diet. Increased gape size with fish growth often contributes to an increase in the range of prey sizes consumed as predator size increases (Scharf et al. 2000). Therefore, we hypothesized that maximum prey size would increase with sablefish size and minimum prey size would remain fairly constant, as seen for other generalist consumers (Scharf et al. 2000). Furthermore, juvenile fishes often shift from predominantly invertebrate prey to piscivory as they grow to adulthood (Mittelbach & Persson 1998).

Methods

Study Area

This study was conducted in St. John Baptist Bay (SJBB), a shallow bay (depth 20-73 m) on Baranof Island, Alaska (57°17'0"-57°17'50" N; 135°33'0"-135°35'0" W). The mouth of the bay opens to Salisbury Sound and SJBB has a freshwater input sourced from the head of the bay. We selected SJBB as a site with potentially high densities of juvenile sablefish based on previous research by the National Marine Fisheries Service (NMFS; Rutecki & Varosi 1997). Nearshore surveys were conducted by NMFS from 1985-1991 throughout Southeast Alaska to determine reliable monitoring sites for juvenile sablefish (Rutecki & Varosi 1997). Out of 74 sampling sites and seven years, SJBB was the only location juvenile sablefish were found consistently and the bay continues to be sampled annually during the NMFS juvenile sablefish tagging survey (Rutecki & Varosi 1997).

Field Sampling

To assess temporal variation in diets, stomach contents were collected from sablefish age 0-2 within SJBB over 5 sampling periods: 12-16 July 2012 (N=302), 20-23 September 2012 (N=271), 13-17 May 2013 (N=4), 8-12 July 2013 (N=391), and 14-17 September 2013 (N=117). Juvenile sablefish were collected from small research vessels by angling at depths of 18-90 m using squid-baited hooks (size 1/0 J-hooks) during day trips. Captured fish were anesthetized by placement into a concentration of 50-80 mg MS-222 per liter of seawater for approximately 5 minutes. Gastric lavage, established as an effective, non-lethal technique to retrieve stomach contents, was used on anesthetized sablefish (Kamler & Pope 2001). Gastric lavage was done by inserting a stream of water into the stomach of the fish through the mouth and rinsing stomach contents out into a sieve. To assess the relationship between diet composition and juvenile sablefish size, fork length (FL; mm) and weight (g) were measured. After gastric lavage and measurements, external plastic-coated wire spaghetti tags (Floy T-bar anchor) were inserted into the dorsal musculature of each fish. Fish were placed into a recovery tank with fresh seawater for approximately 15 minutes to facilitate recovery before returning to their original capture location. Due to field logistics, stomach contents were frozen in July 2012 and July 2013 and preserved in 80% EtOH solution in September 2012 and September 2013. Preservation methods were consistent within a sampling period. Prey mass was not statistically compared across sampling periods because of the differing preservation methods.

In the laboratory, a blotted wet weight (to the nearest 0.01 g) was obtained for total mass of prey in each stomach and for individual prey items. Prey items were counted, identified to the lowest possible taxonomic level, and measured (standard length, SL mm; if possible). Lowest taxonomic level was determined using identification guides specific to the North Pacific Ocean

(e.g. Butler 1980, Kozloff & Price 1996, Smith & Johnson 1996, Shanks 2001, Mecklenburg et al. 2002) and a prey reference collection from intact specimens.

Analytical Methods

For quantitative analyses, the sampling period May 2013 was excluded due to low sample size (N=4). Differences in sablefish size between seasons within each year were determined using a one-way ANOVA and significance was accepted at $\alpha=0.001$. To address the first objective of quantifying taxonomic diversity in diets, cumulative prey curves were plotted for each sampling period (July 2012, July 2013, September 2012, and September 2013) (Ferry & Cailliet 1996). Each curve shows the cumulative number of unique prey taxa identified against the number of stomachs sampled; the asymptote of the curve represents the taxonomic diversity of prey for the sampled predator population. The sample order was randomized 100 times to reduce bias due to the order in which samples were processed and the mean curve was plotted for each sampling period (Ferry & Cailliet 1996). To define the diet composition of juvenile sablefish for each sampling period, prey taxa were quantified by (1) the frequency of occurrence (FO) of each prey taxon, calculated as the number of samples containing prey taxon *i* divided by the total number of sampled sablefish, (2) the proportion of prey taxon by weight (W), calculated as the total weight of prey taxon *i* divided by the total weight of all taxa, and (3) the proportion of prey taxon by number (N), calculated as the count of prey taxon *i* divided by the count of all prey taxa (Chipps & Garvey 2007). These three metrics emphasize different aspects of diet and together describe important prey contributing to diet (Chipps & Garvey 2007). Furthermore, standardizing the prey weights to proportions within a sampling period enabled comparisons of the qualitative differences in diet by weight among sampling periods.

The second objective of this study addressed the temporal variation in prey resource use by juvenile sablefish and their use of seasonally pulsed prey. Quantifying prey taxa by frequency of occurrence, weight, and number provided initial insight into observed differences in important prey among periods. Multivariate analyses were then used to test for statistical differences in diet composition among seasons and years and identify prey taxa that account for differences in diets (Clarke & Gorley 2006; PRIMER v6). For multivariate analyses, taxonomic groups of family level or higher were used to reduce bias due to differences in the taxonomic resolution with which prey were identified. Unknown teleost and invertebrate prey were not included and sablefish with empty stomachs were not included in multivariate analyses. Sampling periods used in analyses were: July 2012, July 2013, September 2012, and September 2013. Analysis of similarity (ANOSIM) was used to test for significant temporal differences in diet composition (Clarke & Gorley 2006). ANOSIM compares within group and between group similarities to test for differences among groups (Clarke & Warwick 2001). ANOSIM tests were performed on a pairwise resemblance matrix calculated using the Jaccard distance measure and prey presence/absence data (Clarke & Gorley 2006). Prey mass was not compared across sampling periods due to different sample preservation methods; samples in EtOH tended to be lower weight than the same samples frozen. ANOSIM tests were performed to determine if there were significant differences between sampling period (July 2012, July 2013, September 2012, and September 2013), season (summer: July 2012 & 2013; fall: September 2012 & 2013) and year (2012 and 2013). To determine potentially important seasonal prey taxa, similarity percentages (SIMPER) were used to determine which prey taxa contributed most to dissimilarities among sampling periods based on prey presence/absence (Clarke 1993).

To compare the energetic quality of the resources being exploited among sampling periods, the energy density of an average sablefish diet was estimated as:

$$\sum_{i=1}^{n} P_i * E_i$$

where n is the total number of prey taxa in the diet, P_i is the proportion by weight of prey taxon i, and E_i is the energy density of prey taxon i (kJ/g wet weight). Invertebrate and teleost prey energy densities were obtained for North Pacific and Gulf of Alaska species published by Cauffopé & Heymans (2005), Anthony et al (2000), and Foy & Norcross (1999). Energy densities vary widely within species and this calculation does not account for the amount of the resource that is assimilated, but serves as a general comparison of energy obtained among sampling periods (Anthony et al. 2000).

To evaluate the prey sizes exploited over all sampling periods, invertebrate and teleost prey lengths (SL) were measured. To test for ontogenetic shifts in teleost prey size, quantile regression was used to define the relationship between teleost prey length and juvenile sablefish length (Scharf et al. 2000). Determining whether the range of prey sizes consumed widens with increased predator size can provide insight into gape limitation and trophic niche breadth (Scharf et al. 2000). This analysis included only teleost prey items for which a length measurement was possible.

Results

A total of 1,081 sablefish (226 mm-455 mm FL) were sampled between July 2012 and September 2013. In both 2012 and 2013, mean sablefish FL (±SD) in September (2012: 366±21 mm, 2013: 370±29 mm) was higher than in July (2012: 325±23 mm, 2013: 334±19 mm;

ANOVA; $p<0.001$; Figure 1.1). This size range corresponds to age 0-2 fish, although 93% of fish sampled fell within the size range of age 1 fish (Rutecki & Varosi 1997). In September 2012, 16 fish were recaptured that were tagged in July 2012, and in September 2013, 8 fish were recaptured from July 2013. Mass-specific growth rates over the two month period between recaptures were 0.0046±0.001 g/g/d in 2012 and 0.0063±0.001 g/g/d in 2013 (Isely & Grabowski 2007). No recaptures occurred between years (Table 1.1).

To describe the composition of juvenile sablefish diets, a total of 2,662 prey items grouped into 48 invertebrate and vertebrate prey taxa were identified (45% to species level, 9% to family level, Table 2). During all sampling periods there was occasional regurgitation at the surface before lavage, which was captured with a net when possible and included in analyses. The majority of regurgitated prey was Pacific herring. Across all sampling periods, Pacific herring was the dominant prey type by weight (55%), followed by salmonid offal (16%) and smelts (osmerids combined, 7%). Salmonid offal included skin, bones, organs and eggs from moribund salmon and salmon carcasses washed into SJBB from the inlet creek subsequent to spawning. Krill (Euphausiidae) were the only invertebrate prey group that contributed >1% of the diet by weight (5%). Most of the dominant prey items by % weight also had a high frequency of occurrence in sablefish sampled, with the most frequently occurring taxa being Pacific herring (49%), salmonid offal (14%), and krill (Euphausiidae ,13%). Krill were the most numerically abundant prey (90%); however, large numbers of krill were consumed in only one sampling period (September 2012). In all sampling periods, algae and terrestrial leaf litter accompanied prey items in stomachs.

To describe temporal variation in resource use by sablefish, diets were compared across sampling periods. Qualitatively, the number of fish sampled and the percentage of fish that

contained stomach contents varied among sampling periods with fall sampling trips yielding a higher proportion of fish with stomachs containing prey items than in summer (excluding May 2012, Table 1.1). The cumulative prey curve for each sampling period increased at a different rate without reaching a clear asymptote even when close to 300 fish were examined (Figure 1.2), confirming the opportunistic feeding behavior of juvenile sablefish. The average number of prey taxa in 100 stomachs sampled ranged from 10 in July 2013 to 25 in July 2012, showing that across periods there seemed to be differences in taxonomic diversity of diets. The taxonomic diversity of sampling periods in July and September 2012 was qualitatively higher than in 2013, based on cumulative prey curves (Figure 1.2). Across sampling periods there was variation in the dominant prey taxa based on number, frequency of occurrence and weight (Table 1.2).

Sablefish diets differed significantly among sampling periods (ANOSIM; Global R=0.278, p<0.001) (Table 1.3). Pairwise tests revealed that all sampling periods were significantly different from each other (ANOSIM; Table 1.3). Diet composition was significantly different between years and between seasons (ANOSIM; year: R=0.165, p<0.001; season: R=0.094, p<0.001) (Table 1.3). Based on SIMPER, the largest differences among sampling periods were due to variation in occurrence of Pacific herring, salmonid offal and krill (Table 1.4). Diet quality, in terms of energetic content and weight, was highest in September 2013 (7 kJ/g), intermediate in September 2012 and July 2013 (5 kJ/g), and lowest in July 2012 (4 kJ/g) (Table 1.1). The higher ration size and high energetic content of salmonid offal (Hilderbrand et al. 2004) suggests greater energy intake by sablefish in September 2013 (Figure 1.3).

The qualitative differences among sampling periods were evident when comparing the important prey groups (Table 1.2). In July 2012, the majority of stomachs contained invertebrate prey, with the most frequently occurring groups being larval crabs (Brachyura, 16%), molted

barnacle exoskeletons (Cirrepedia, 11%) and amphipods (Gammaridea and Hyperiidea, 10%). By frequency of occurrence, the most common fish prey was Pacific herring (9%). By number, 71% of the diet was composed of invertebrates, with larval crabs making up 20% of the diet. Although invertebrates were abundant and occurred frequently in stomachs in July 2012 samples, the diet by weight was dominated by fishes (80%), particularly Pacific herring (28%) and cod (Gadidae, 21%). Worms, including polychaetes and sipunculids, composed 11% of the total diet by weight.

In September 2012, the diets appeared less diverse overall and were dominated by Pacific herring, krill, and salmonid offal. Pacific herring occurred in 43% of fish sampled in this period and made up 38% of the diets by weight. This was the only sampling period in which krill were found in substantial quantities (FO: 49%, N: 97%, W: 18%). Salmonid offal was found in 17% of the stomachs and made up 14% of the diet by weight. In addition to finding salmonid offal in the stomachs, we observed numerous pink salmon returning to spawn at the time of sampling within SJBB. The majority of the diet by all three metrics was made up of Pacific herring in July 2013 (FO: 74%, N: 68%, W: 82%). Smelts occurred in 9% of the samples and contributed 8% of the diet by weight and 6% by number.

In contrast to July 2012, sablefish stomachs sampled in July 2013 appeared to have lower prey diversity and invertebrate prey taxa only occurred in 5% of the sampled stomachs based on cumulative prey curves. Samples from September 2013 were qualitatively the least taxonomically diverse. In September 2013, salmonid offal was the most important prey item by frequency of occurrence and weight (65% and 55%, respectively). Pacific herring were the most numerically abundant (38%), occurred in 50% of the samples, and composed 33% of the diet by weight.

Prey size was also quantified and compared with predator size to describe ontogenetic shifts in diet. Prey lengths ranged from 0.1 mm to 204.7 mm and sampled sablefish consumed prey up to 60% of their body length (FL) (Figure 1.4). The upper and lower bounds of the length-based quantile regression showed no significant increasing or decreasing trend in teleost prey size with predator ontogeny (N=727; 5^{th} quantile: β=-0.085, P =0.118) (N=727; 95^{th} quantile: β=-0.014, P =0.948). The majority of Pacific herring consumed by juvenile sablefish fell within the size range observed for YOY (Norcross et al. 2001); however, the Pacific herring consumed in fall sampling periods were generally smaller than those consumed in summer (Figure 1.5).

Discussion

Overall, juvenile sablefish exploit a large variety of prey taxa characteristic of a generalist predator, with significant diet shifts between sampling periods revealing seasonal and interannual variation in resource use (Figure 1.3). Diets were more diverse, with more invertebrate taxa in 2012 than in 2013, when Pacific herring and salmonid offal dominated diets. The energetic quality of the diet, prey mass, and sablefish growth rate were all lower in 2012 than 2013, suggesting that the nutritional condition of sablefish may vary across years. Juvenile sablefish are capable of taking advantage of seasonally available, high energy prey within SJBB, based on the quantity of salmonid offal in the diets. The July 2012 sampling period was particularly distinct, with a higher proportion of empty stomachs observed and higher occurrence of relatively low-weight and low-energy invertebrate species. During this sampling, we may have observed a period when high-energy prey was sparse. Prey availability may influence the differences in diet composition and proportion of empty stomachs between seasons, but we are

unable to evaluate the functional response of sablefish to their prey due to limited information about in situ prey resource abundance. The fish and invertebrate community composition has not been characterized for SJBB and the bay is relatively understudied despite its importance as rearing habitat for commercially valuable species, such as sablefish, pacific herring, and pink salmon (Rutecki & Varosi 1997, Piston & Heinl 2011).

In Alaskan waters, previous studies have characterized diets for larval and YOY sablefish (90 -200 mm) and sablefish >400 mm (Grover & Olla 1990, Yang & Nelson 2000, Sigler et al. 2001). The current study fills a gap in knowledge of sablefish feeding ecology by providing diet information for sablefish ranging from 226 to 455 mm in length. Sigler et al. (2001) found that YOY diets were dominated by krill (%W) and other zooplankton, while only larval-stage fish were consumed. In the current study, a high proportion of the diet for all sampling periods by weight for sablefish was pelagic fish, primarily Pacific herring. Clear ontogenetic shifts in diet were not observed over the range of sablefish sizes sampled in the current study; however, comparing our results with previous studies suggests that juvenile sablefish switch to a diet dominated by teleost prey between age 0 and 1, while the adults predominantly consume fish and cephalopods (Yang & Nelson 2000).

Although diet composition varied seasonally and between years sampled, forage fish, such as Pacific herring and smelts, were a consistent component of the diet. As for many marine predators, Pacific herring were the most important prey in juvenile sablefish diet by weight and frequency of occurrence. Although sablefish were larger in fall, they were consuming smaller Pacific herring than in summer, suggesting that environmental factors were accounting for variation in prey fish size instead of ontogeny within the predator size range sampled. This is corroborated by the lack of significant trend between prey size and predator size. Pacific herring

were found in stomachs during all sampling periods; however, in July 2012 there was a markedly low frequency of Pacific herring occurrence in the diet compared with other periods. Pacific herring stock biomass was not considered low in 2012 within this region of Southeast Alaska (Hebert 2013), and the sparse occurrence in the diets in July may be due to the timing of sampling. For example, Pacific herring may not have been present within the bay during the days sampled, although this information is not known.

The lack of salmonid offal in the diets during July sampling periods, paired with the known seasonal migration patterns of Pacific salmon, suggests that juvenile sablefish are taking advantage of this pulsed resource when it is available. The only sampling period in which forage fish made up < 50% of the diet by weight was September 2013, when the majority of the diet was composed of scavenged salmon. We estimated the highest energy diet for juvenile sablefish during this period, and growth rate was higher in 2013, though growth rate between years was not significant. Pacific salmon pulses have been widely documented to be a beneficial source of marine derived nutrients to terrestrial predators, such as bears, wolves, foxes, and martens; freshwater predators, such as Arctic grayling, Dolly Varden, and rainbow trout; and avian predators, such as eagles, gulls, crows, and ravens (Willson & Halupka 1995, Schindler et al. 2003, Bentley et al. 2012). Documentation of marine predators exploiting adult spawning salmon pulses in the nearshore has primarily focused on mammals including seals, sea lions, and cetaceans (Willson & Halupka, 1995, Saulitis et al. 2000, Sinclair & Zeppelin 2002). Although nearshore marine fish species are known to exploit out-migrating juvenile salmon (e.g. Sturdevant et al. 2009), the current study is one of the first to document a marine fish species scavenging on adult salmon carcasses in coastal marine waters. Thus, this study further emphasizes the significance of salmon as a vector of energy across ecosystems and indicates a

need for continued research to better understand the importance of spawning salmon to marine predators.

While we could not definitively identify consumed salmon to species, we observed many moribund mature pink salmon, *O. gorbuscha*, at the surface of the water in SJBB during fall sampling periods. Based on field observations and known timing of pink salmon returns to this region from late July to late September (Smoker et al. 1998, Piston & Heinl 2011), it is likely that this species accounts for a high proportion of the salmonid offal observed in sablefish diets. Pink salmon stocks in Southeast Alaska have had dominant odd-year run strength since 1999, with poor even-year runs since 2006 that exaggerate this cyclicity (Piston & Heinl 2011). In 2013, Southeast Alaska had the second highest pink salmon harvest on record and a large return was predicted due to previously favorable ocean conditions for these fish as juveniles (Figure 1.6) (ADFG 2013). The occurrence of a vastly larger pink salmon run size in 2013 than 2012 may explain the higher contribution of salmonid offal to the diet of juvenile sablefish in 2013.

Energy gained by sablefish at the juvenile life stage from high quality prey, such as salmon and Pacific herring, can translate into growth or lipid storage. Other fishes such as rainbow trout and arctic grayling experience significantly increased ration size and growth rate as a result of increased salmon densities (Bentley et al. 2012). Average ration size increased by up to 491% for Arctic grayling and 200% for rainbow trout when sockeye salmon densities were high in two freshwater streams, and rainbow trout switched to a diet of almost entirely salmon (Bentley et al. 2012). In locations where resources may be limited in winter, energy allocation in fishes can switch from growth to lipid storage in the fall (Sogard & Spencer 2004). In May 2013, sampling occurred when water temperature was 3°C, which may be near the lower metabolic threshold for juvenile sablefish. In lab experiments, juvenile sablefish exposed to temperatures <

2°C for longer than 60 seconds experienced a loss of equilibrium followed by mortality (Sogard & Olla 1998). The four fish caught in May were lethargic, with only one individual containing a sparse amount of prey, suggesting that sablefish may not feed as actively within SJBB during colder periods. In juveniles, both increased lipid storage and growth are beneficial for overwinter survival, and allocation of energy towards one physiological function may require sacrificing an increase in the other (Post & Parkinson 2001, Sogard & Spencer 2004). Although this tradeoff exists, juvenile sablefish provided high rations and optimal conditions in a laboratory setting did not exhibit a tradeoff between lipid storage and growth; instead storage and growth were positively correlated (Sogard & Spencer 2004). Thus, consumption of high energy prey by sablefish during the summer and fall may be particularly important for maintaining good condition as they enter the winter period of low productivity.

Many consumers opportunistically shift their diets to a high proportion of a pulsed resource; for example, damselfish specialize on coral propagules during coral spawning events (McCormick 2003). Similarly, sablefish in SJBB may specialize on salmon during their spawning migrations. While high-energy prey like Pacific herring and salmon are important to sablefish nutrition, these pulsed resources are ephemeral. In contrast, benthic invertebrates such as worms, gammarid amphipods, and clams are more regularly available *in situ* but are of lower quality. The ability of sablefish to exploit a large variety of autochthonous and allochthonous prey suggests that they are not solely dependent on the influx of spawning salmon, but that the pulse may contribute to overwinter survival and rapid juvenile growth. However, evaluating the potential for pulsed resources to confer population-level benefits to sablefish requires continued investigation into the relationships between energy consumption, growth, and survival of juvenile sablefish. Moreover, sampling for 4-5 days each month provided a snapshot of sablefish

diet within SJBB that may not be representative of the entire summer or fall. Juvenile sablefish feeding ecology should be studied in SJBB and other nearshore habitats on a longer temporal scale (i.e., additional seasons and years) to better reveal the dynamic nature of their resource use, for example, through the use of stable isotopes. Thoroughly understanding consumer-resource relationships of juvenile sablefish can provide insight into how they will respond to anthropogenic and environmental disruptions to resource abundance in the North Pacific Ocean and coastal marine habitats.

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Figures

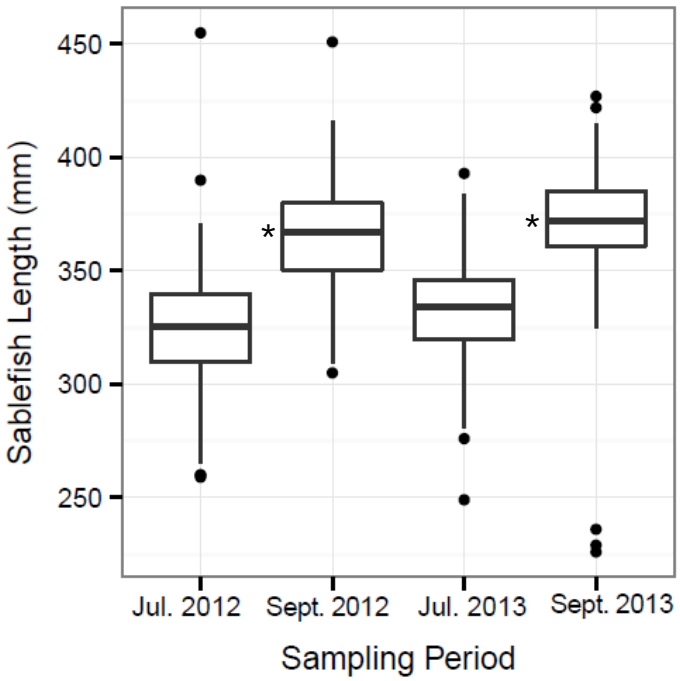

Figure 1.1 Boxplots depicting the range in lengths (fork length in mm) of sablefish collected by sampling period. The top and bottom of each box represents the 75th and 25th percentile while the line inside the box is the median sablefish length. Vertical lines ("whiskers") represent 1.5 x the inter-quartile range from the upper and lower box edges and closed circles represent outliers that fall beyond this range. Asterisks next to boxes in September of 2012 and 2013 represent significant differences between July and September of each year (ANOVA; p<0.001).

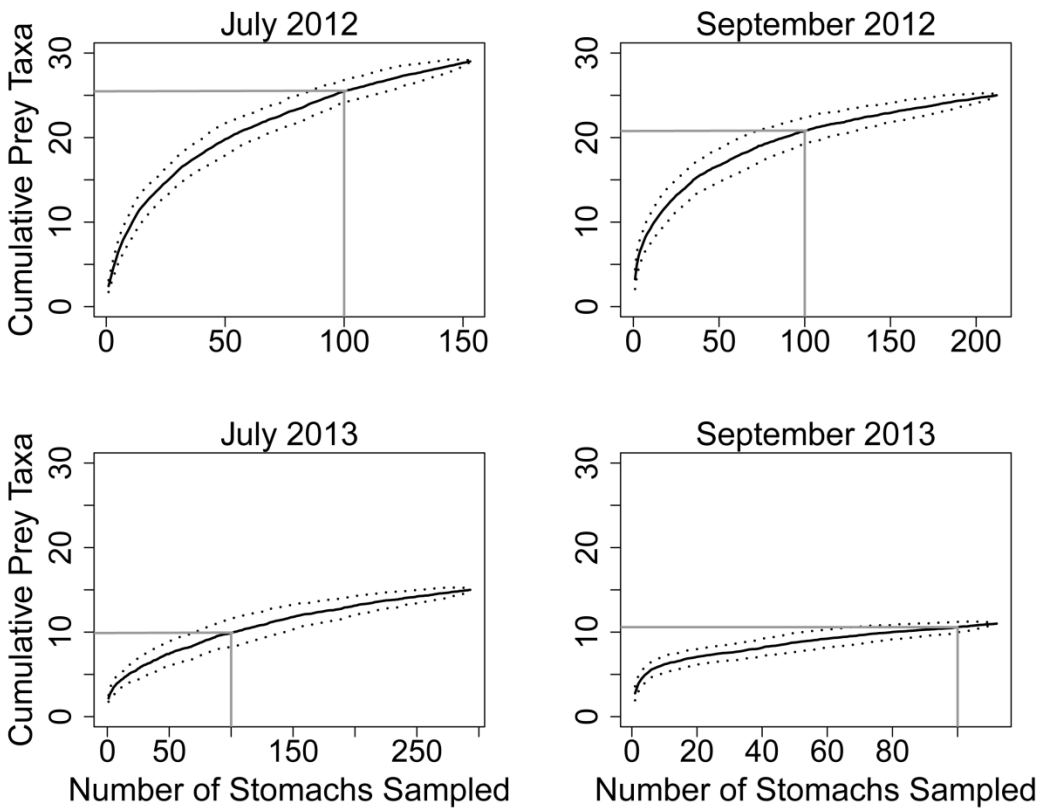

Figure 1.2 Cumulative prey curves for sablefish sampled in July 2012 (n=165), September 2012 (n=219), July 2013 (n=299) and September 2013 (n=113). The solid line represents the mean cumulative number of unique prey taxa based on randomizing the order in which stomachs were sampled 100 times. The dotted lines represent the standard deviation. To compare sampling periods, gray vertical and horizontal lines signify the mean number of cumulative prey taxa at 100 stomachs sampled (July 2012=25, September 2012=21, July 2013=10, September 2013=11).

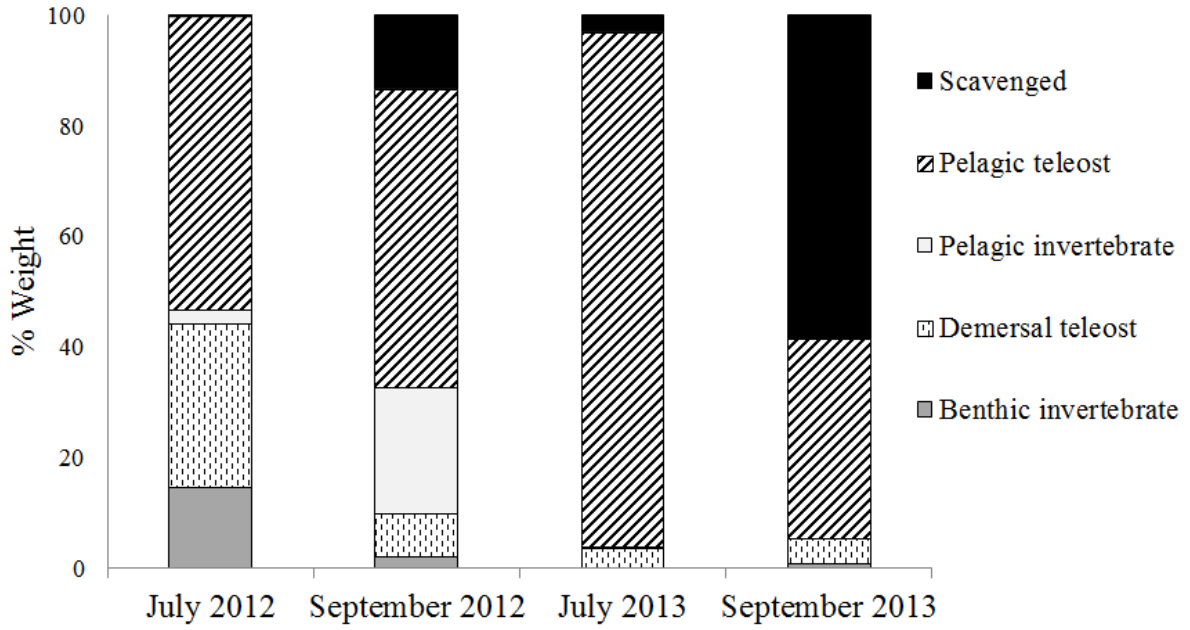

Figure 1.3 Diet composition by % weight across sampling periods (July 2012, n=356; September 2012, n=841; July 2013, n=415; September 2013, n=204). Unknown fish and invertebrate prey were excluded from the plotted prey categories by weight as they did not fit within one specific group.

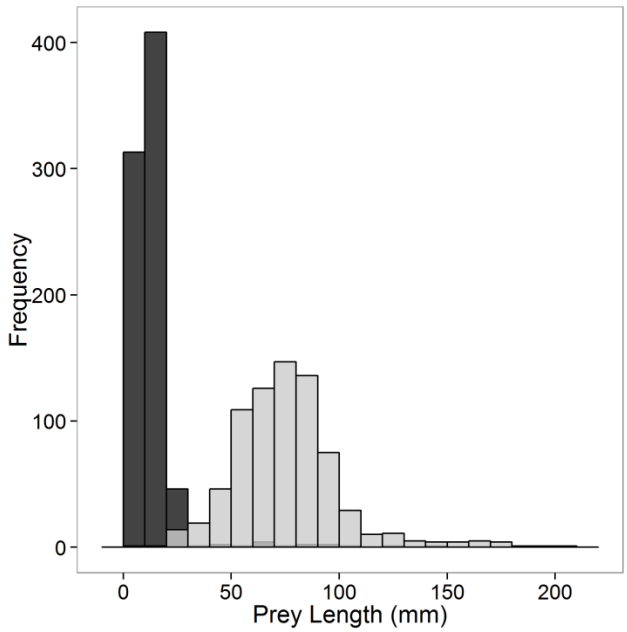

Figure 1.4 Frequency distribution of prey lengths (mm) grouped by invertebrate prey (black) and fish prey (gray), in 10 mm increments (seasons combined, n=1,532).

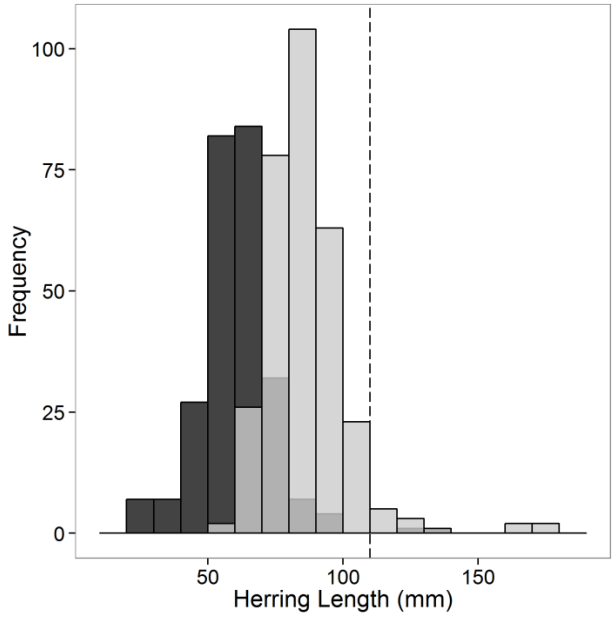

Figure 1.5 Frequency distribution of Pacific herring prey lengths (mm SL) by season (combined sampling periods; n=568), in 10 mm increments. Black bars represent fall Pacific herring prey lengths, light gray bars represent summer Pacific herring prey lengths, and dark gray bars indicate overlap between fall and summer length distributions. The vertical dashed line is the mean size for age-1 Pacific herring (110 mm; Norcross et al., 2001).

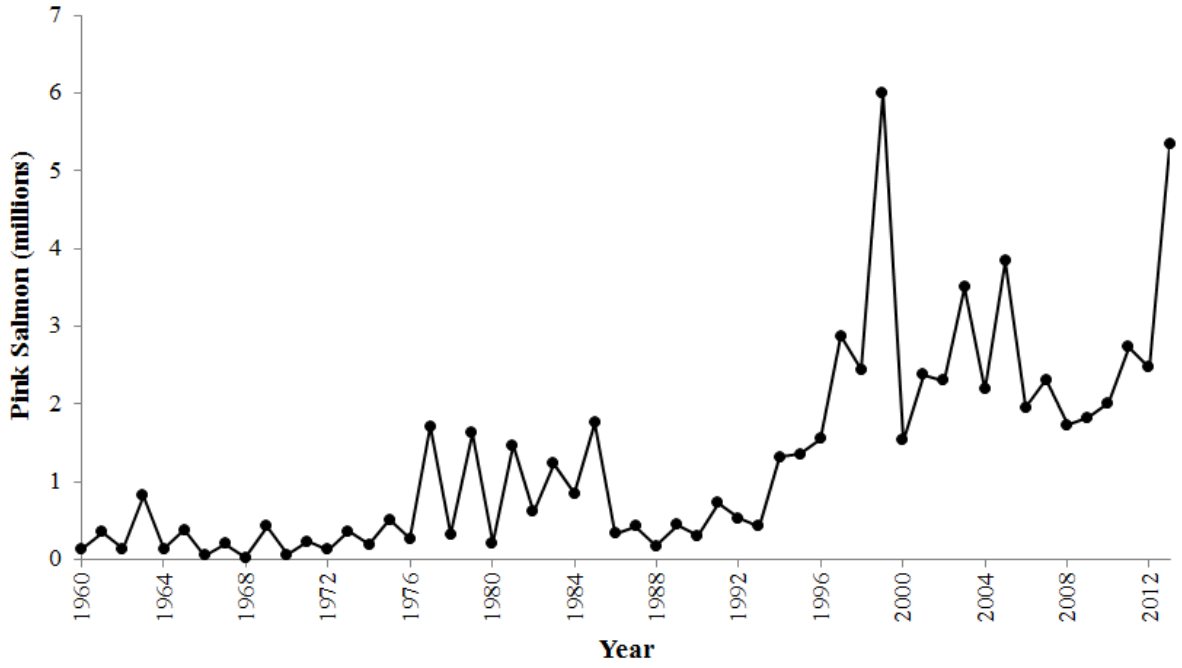

Figure 1.6 Pink salmon escapement index for the northern outside region of Southeast Alaska, including St. John Baptist Bay. Pink salmon are regionally cyclic in abundance and had anomalously high harvest and escapement in 2013 (Piston and Heinl, 2011). Data were provided by A. Piston, Alaska Department of Fish and Game, 17 April, 2014.

Tables

Table 1.1 Summary of total fish sampled, proportion of fish containing prey, mean growth rate of recaptured fish, mean relative prey mass (ration size), and calculated energy density of all prey by sampling period. May 2013 calculations were not included because only 1 out of 4 fish contained stomach contents. Mean mass-specific growth rate was calculated using fish that were recaptured in September 2012 (n=13) and September 2013 (n=8).

Sampling period	Number of fish sampled	Fish with stomach contents (%)	Mean (SD) mass-specific growth rate (g/g/d)	Mean (SD) ration size (% body weight)	Energy density of diet (kJ/g)
July 2012	302	58	0.0046 (0.001)	0.2 (0.65)	4
Sept 2012	271	95		0.2 (0.50)	5
May 2013	4	25	---	---	---
July 2013	391	80	0.0063 (0.001)	0.7 (0.94)	5
Sept 2013	117	97		0.6 (0.79)	7

Table 1.2 Diet composition of juvenile sablefish in SJBB for sampling periods July 2012 (n=165), September 2012 (n=219), July 2013 (n=299) and September 2013 (n=113). Diet composition was quantified by percent frequency of occurrence (%FO), weight (%W), and number (%N). The taxonomic level in which prey items were identified varied and the first column ("Prey Taxa") represent the lowest taxon that could be identified. The energy density values from the literature (rounded to nearest kJ/g WW) used to estimate the energetic quality of the diet are shown for each prey taxa. Unknown fish and invertebrates were assigned the average energy density of all identified teleost taxa and invertebrate taxa. For salmonid offal energy contribution, roe, spawned, and ripe salmon densities were averaged.

	July 2012			September 2012			July 2013			September 2013			Energy Density
Prey Taxa	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	kJ/g
Fishes													
Ammodytes hexapterus	—	—	—	0.47	0.35	0.01	—	—	—	—	—	—	6[1]
Clupea pallasi	8.5	28.22	4.21	43.4	37.76	1.09	73.63	81.88	68.46	50	33.29	38.1	5[1]
Cottidae	0.65	0.34	0.28	—	—	—	—	—	—	—	—	—	4[1]
Leptocottus armatus	—	—	—	0.47	4.02	0.01	—	—	—	—	—	—	4[1]
Gadidae	2.61	2.57	1.4	2.83	1.17	0.04	0.68	1.38	0.4	4.46	0.78	1.83	3[1]
Microgadus proximus	1.96	18.39	0.84	0.47	0.46	0.01	0.34	1.54	0.2	2.68	1.58	1.1	3[1]
Gadus chalcogrammus	—	—	—	—	—	—	—	—	—	0.89	1.84	0.37	3[1]

[1]Anthony *et al*, 2000; [2] Caffoupé and Heymans, 2005; [3]Foy and Norcross, 1999; [4]Hilderbrand *et al*, 2004; *not included in energetic quality of the diet

Table 1.2 Continued

	July 2012			September 2012			July 2013			September 2013			Energy Density
Prey Taxa	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	kJ/g
Hexagrammidae	0.65	1.77	0.28	—	—	—	0.34	0.36	0.2	—	—	—	4[1]
Osmeridae	0.65	2.76	0.28	8.96	6.04	0.15	7.19	4.42	5.19	1.79	1.11	0.73	6[1]
Mallotus villosus	0.65	4.91	0.28	0.47	0.31	0.01	1.37	3.42	1	—	—	—	5[1]
Thaleichthys pacificus	0.65	8.6	0.28	0.47	1.08	0.01	—	—	—	—	—	—	7[1]
Pleuronectidae	—	—	—	0.47	0.17	0.01	—	—	—	—	—	—	4[1]
Teleostei, unid.	30.07	13.87	12.92	51.42	12.56	0.79	25.34	3.84	16.37	26.79	4.14	12.09	5
Invertebrates													
Crustaceans													
Crustacea	6.54	0.21	2.81	0.94	0.05	0.01	—	—	—	0.89	0.41	0.37	4[2]
Amphipoda	0.65	0	0.28	3.77	0.02	0.07	0.34	0	0.2	—	—	—	3[2]
Gammaridea	2.61	0.05	2.25	1.42	0	0.05	0.34	0	0.2	—	—	—	3[2]
Hyperiidea	7.19	0.14	3.37	2.83	0.02	0.09	2.74	0.02	5.39	0.89	0	0.37	3[2]
Copepoda	1.31	0.29	20.51	5.66	0.01	0.09	—	—	—	—	—	—	2[2]
Decapoda	0.65	0.05	3.65	0.94	0	0.01	—	—	—	—	—	—	4[2]
Caridea	0.65	0.02	0.28	1.89	0.03	0.03	—	—	—	—	—	—	5[2]
Dendrobranchiata	0.65	0.03	0.56	—	—	—	—	—	—	—	—	—	5[2]
Oplophoridae	0.65	0.03	0.56	—	—	—	—	—	—	—	—	—	5[2]
Penaeidea	1.31	0.04	0.56	—	—	—	—	—	—	—	—	—	5[2]
Larval Crustaceans													
Brachyura (Zoea)	3.92	0.11	7.87	—	—	—	—	—	—	—	—	—	3[3]

[1]Anthony *et al*, 2000; [2] Caffoupé and Heymans, 2005; [3]Foy and Norcross, 1999; [4]Hilderbrand *et al*, 2004; *not included in energetic quality of the diet

Table 1.2 Continued

	July 2012			September 2012			July 2013			September 2013			Energy Density
Prey Taxa	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	kJ/g
Anomura	0.65	0	0.28	0.47	0	0.01	—	—	—	—	—	—	3[3]
Cancridae	3.27	0.26	1.4	—	—	—	—	—	—	—	—	—	3[3]
Fabia subquadrata	0.65	0	0.28	—	—	—	—	—	—	—	—	—	3[3]
Pinnotheridae	7.19	0.14	9.55	—	—	—	—	—	—	—	—	—	3[3]
Portunidae	0.65	0	0.28	—	—	—	—	—	—	—	—	—	3[3]
Euphausiacea	—	—	—	—	—	—	0.34	0.01	0.2	—	—	—	5[2]
Euphausia pacifica	—	—	—	48.58	17.78	96.55	—	—	—	—	—	—	5[2]
Other Invertebrates													
Bivalvia	—	—	—	2.83	0.01	0.04	—	—	—	—	—	—	2[2]
Limidae	0.65	0.02	0.56	—	—	—	—	—	—	—	—	—	2[2]
Cephalopoda	—	—	—	—	—	—	0.34	0.15	0.2	0.89	0.12	0.37	4[2]
Ctenophora	9.8	1.24	5.62	1.89	0.73	0.02	1.03	0.13	0.6	—	—	—	0[2]
Gastropoda	—	—	—	1.89	0.02	0.04	—	—	—	—	—	—	2[2]
Holothuroidea	1.31	0.7	0.56	—	—	—	—	—	—	—	—	—	1[2]
Nematoda	0.65	0	0.28	—	—	—	—	—	—	—	—	—	0[2]
Polychaeta	0.65	0.32	0.28	—	—	—	—	—	—	0.89	0.21	0.37	3[2]
Nereididae	1.96	7.79	0.84	—	—	—	—	—	—	0.89	0.56	0.37	3[2]
Echiuridae	—	—	—	0.94	1.52	0.01	—	—	—	—	—	—	3[2]
Pycnogonida	0.65	0	0.28	—	—	—	—	—	—	—	—	—	4[3]
Salpidae	1.31	0.14	0.56	—	—	—	—	—	—	—	—	—	0[2]

[1]Anthony *et al*, 2000; [2] Caffoupé and Heymans, 2005; [3]Foy and Norcross, 1999; [4]Hilderbrand *et al*, 2004; *not included in energetic quality of the diet

Table 1.2 Continued

	July 2012			September 2012			July 2013			September 2013			Energy Density
Prey Taxa	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	%FO	%W	%N	kJ/g
Sipunculidae	1.31	2.83	0.56	0.47	0.4	0.01	—	—	—	—	—	—	2[2]
Invertebrate, unid.	1.96	0.11	0.84	6.13	0.64	0.08	0.34	0	0.2	—	—	—	3
Teleostei	—	—	—	—	—	—	1.37	2.83	0.8	—	—	—	5[1]
Cirripedia (molted exoskeleton)	11.11	0.12	5.9	0.94	0	0.01	—	—	—	—	—	—	0[2]
Other													
Algae and terrestrial leaf litter	19.61	3.9	8.43	41.04	0.81	0.54	0.68	0.03	0.4	31.25	1.27	12.82	0*

[1]Anthony *et al*, 2000; [2] Caffoupé and Heymans, 2005; [3]Foy and Norcross, 1999; [4]Hilderbrand *et al*, 2004; *not included in energetic quality of the diet

Table 1.3 Results of two-way crossed analysis of similarity (ANOSIM) testing for differences between seasons and years. One way ANOSIM pairwise comparisons were made to determine significant differences among sampling periods. ANOSIM tests were based on presence/absence diet data, with 9999 permutations and significance set at α=0.01.

Analysis of Similarity based on Presence/Absence		
2 way ANOSIM test	Global *R*	*P*
Year	0.305	<0.001
Season	0.267	<0.001
ANOSIM Sampling Period Pairwise tests	*R*	*P*
July 2012, September 2012	0.217	<0.001
July 2012, July 2013	0.382	<0.001
July 2012, September 2013	0.179	<0.001
September 2012, July 2013	0.268	<0.001
September 2012, September 2013	0.167	<0.001
July 2013, September 2013	0.305	<0.001

Table 1.4 Results of similarity percentages (SIMPER) analyses determining the overall dissimilarity between sampling periods (%) and identifying the primary prey groups contributing to those differences. Contributing prey groups listed make up 90% of the dissimilarity for each pair of sampling periods.

	July 2012 September 2012	**July 2012 July 2013**	**September 2012 September 2013**	**July 2013 September 2013**	**September 2012 July 2013**	**July 2012 September 2013**
Mean Dis. (%)	97	94	80	72	76	97
Group Contribution to difference (%)						
Clupeidae	22	48	27	40	40	25
Salmonid offal	8	—	32	43	9	35
Euphausiidae	21	—	20	—	25	—
Brachyura	6	7	—	—	—	6
Ctenophora	5	6	—	—	—	5
Cirripedia	5	6	—	—	—	5
Osmeridae	5	6	5	5	9	2
Hyperiidea	3	5	—	—	3	3
Gadidae	3	3	4	5	2	5
Crustacea	3	4	—	—	—	3
Arthropda	3	—	3	—	3	—
Copepoda	2	—	—	—	—	—
Bivalvia	2	—	—	—	—	—
Cancridae	1	2	—	—	—	—
Gammaridea		2	—	—	—	—
Polychaeta	1	2	—	—	—	2

Chapter 2:

Vertical migrations of juvenile sablefish (*Anoplopoma fimbria*) in coastal Southeast Alaska

Abstract

Describing fine-scale movements of juvenile sablefish can provide insight into their mechanisms for survival in nearshore habitats. Juvenile sablefish have been found to eat benthic and pelagic prey, implying potential vertical migration off the bottom to forage, however little is known about their fine-scale movement. This study assessed the vertical movement patterns of juvenile sablefish in relation to daylight and tidal cycles using acoustic telemetry. Thirteen juvenile sablefish were implanted with acoustic transmitters and monitored by 2 acoustic receivers from 5 Oct to 14 Nov 2003 within St. John Baptist Bay, Baranof Island, Alaska. The six fish that remained within range of the receivers spent the majority of time near the bottom, but made periodic vertical excursions. Generalized linear mixed models were used to determine the relationship between excursion frequency and environmental factors. Excursions were influenced by tide and diel conditions, with a higher excursion frequency at dawn and during slack and flood stages and a lower excursion frequency at night. Flood and slack tide may create an influx of pelagic prey resources, which could lead to the more frequent vertical movement of juvenile sablefish during these tidal stages. Higher probability of excursions at dawn may be due to factors such as predator avoidance or increased prey movement at crepuscular periods. To date, this is the first study describing vertical migration of juvenile sablefish in the wild and

reveals that environmental conditions have the potential to affect the fine-scale movements of juvenile sablefish within nearshore habitats.

Introduction

Broad scale sablefish (*Anoplopoma fimbria*) movement throughout the Gulf of Alaska has been studied through tag-recapture studies that have defined a northwestern migration of young mature adults, and older adults moving in a more southeastern direction in gulf waters (Heifetz & Fujioka 1991, Rutecki & Varosi 1997, Maloney & Sigler 2008). Sablefish show ontogenetic shifts in both their large-scale movement patterns and depth distributions. Adults are demersal, inhabiting deep continental slope and outer shelf waters in the Gulf of Alaska and Bering Sea, where they are commercially caught by longlines and pot gear (Rutecki & Varosi 1997, Sigler et al. 2001). They spawn offshore near the continental shelf and eggs have been found at depths >200m (Kendall & Matarese 1987). In contrast, larval and pre-settlement juvenile sablefish are caught in surface trawls in shelf waters and are associated with the neuston layer (Kendall & Matarese 1987). Juvenile sablefish reside in nearshore waters for 1-2 years before reaching maturity and migrating into deeper waters (Rutecki & Varosi 1997). During this time they transition from being neustonic to demersal, though how juveniles are using nearshore habitats during the critical first years of life is not well understood.

Describing fine-scale movements of juvenile sablefish can provide insight into their mechanisms for survival within these nearshore environments. Drivers of vertical migrations by marine organisms are difficult to resolve on small spatial and temporal scales, but migrations can be associated with behaviors such as nest guarding, foraging, and predator avoidance (Clark &

Levy 1988, Sogard & Olla 1998, Nichol & Somerton 2002). Survival of fish at early life stages requires overcoming competition and predation while finding suitable prey. Juvenile sablefish have been found to eat benthic and pelagic prey (Cailliet et al. 1988, Gao et al. 2004, this thesis), implying potential vertical migration off the bottom to forage. Predator avoidance is often associated with low activity and occupation of low light areas (e.g., greater depths) to decrease visibility and chance of encounter with visual predators (Eggers 1978, Loose & Dawidowicz 1994). For example, juvenile sockeye salmon are visual planktivores and make brief excursions into shallower depths to feed during dusk, a behavior that is thought to minimize exposure to predators while still fulfilling energetic requirements (Eggers 1978). Juvenile sablefish may make a similar tradeoff between acquiring food and avoiding visual predators in the water column.

Environmental factors and physiological needs also have the potential to dictate fish vertical movement (Sogard & Olla 1998). Juvenile sablefish distribution throughout the water column in shelf habitats may be influenced by environmental variables such as temperature, currents, tidal fluctuations and diel period. Availability of prey resources, such as zooplankton, often fluctuates with tides and currents, thus influencing foraging-driven vertical migrations of predators (Laprise & Dodson 1989, Frost & Bollens 1992). For example, atka mackerel (*Pleurogrammus monopterygius*) showed increased vertical excursions from the bottom with increased light intensity but decreased excursions during high current velocity associated with spring tides (Nichol & Somerton 2002). In an experimental setting, juvenile sablefish (≤100 mm) varied their vertical distribution according to food availability and were more active during the day than at night; however, this diel trend was less evident as juveniles increased in size (Sogard & Olla 1998). At night, some juveniles were also observed using structures at the bottom of the

tank, potentially as a refuge for resting. Juvenile sablefish also avoided their lower temperature threshold (2°C) and bright light (Sogard & Olla 1998). It is plausible that within the nearshore, juvenile sablefish are impacted by a multitude of environmental variables that dictate their vertical movement.

Although the range of depths inhabited by sablefish throughout their life history have been documented, very little is known about fine-scale patterns in habitat use. In southeast Alaska, juvenile sablefish are consistently found in St. John Baptist Bay (SJBB), Baranof Island, which provides a reliable nearshore habitat to investigate sablefish vertical movement (Rutecki & Varosi 1997, Courtney & Rutecki 2011). This study aimed to 1) assess the vertical movement patterns of juvenile sablefish within SJBB using acoustic telemetry and 2) describe vertical movements in relation to daylight and tidal cycles within SJBB. We hypothesized that juvenile sablefish would be detected throughout the water column due to their benthic and pelagic prey resource use within SJBB (see Chapter 1). Furthermore, we hypothesized that sablefish would be more active during crepuscular periods to exploit prey while avoiding predation and that sablefish would display higher rates of vertical movement in the water column during flood events, due to the potential influx of pelagic prey.

Methods

Sampling and Data Collection

Acoustic telemetry was used to record sablefish movement within St. John Baptist Bay, (SJBB) from 2 October 2003 to 18 November 2003. SJBB is a small bay approximately 3 km in length and < 1km wide, located on the northwestern side of Baranof Island, 39 km north of Sitka,

Alaska (57°17’0”-57°17’50” N; 135°33’0”-135°35’0” W, Figure 2.1). Field techniques, including acoustic receiver setup, range testing, and fish tagging procedures, were described in detail by Courtney and Rutecki (2011). We provide a brief summary of methods here. To remotely detect tagged fish, two moored acoustic receivers (LOTEK MAP-SDL) were located near the head of the bay in bottom depths of 18 m and 21 m at low tide (receiver 1: 57° 17.2 N 135° 33.659 W, receiver 2: 57° 17.12 N 135° 33.648 W).

Age 0+ sablefish were captured by angling, anesthetized using MS-222, and surgically implanted with acoustic transmitters (LOTEK CTP-M11-12: length 45mm, diameter 11mm, frequency 77 kHz, 5 sec transmission rate). Tagged fish were held in flow-through seawater tanks on the research vessel for at least 24 hours to recover and were released near their capture location 1– 2 October 2003 (Courtney and Rutecki, 2011). A total of 13 juvenile sablefish (225-260 mm fork length; FL) were tagged and released within St. John Baptist Bay (57°17.178 N, 135° 33.723 W) (Table 2.1). For each fish detection, acoustic receivers recorded unique tag ID, ambient pressure (converted to depth in meters), date, and time to the nearest 5-second interval. Range detection tests on deployed receivers revealed an average detection range of 206 m, and all 13 tags released were detected at least once after release. Two tagged fish appeared to be mortalities, 5 fish left the region covered by the receivers, and 6 fish remained in the area and were used for our analyses (Table 2.1).

Tidal predictions from October-November 2003 in Neva Strait, adjacent to SJBB, were acquired from the University of South Carolina Biological Sciences department tide predictor (Pentcheff, http://tbone.biol.sc.edu/tide/tideshow.cgi 2003) to determine the tidal stage at the time of fish detection. Daylight data for October-November 2003, including nautical dawn,

sunrise, sunset and nautical dusk, were retrieved from the archives of the Naval Observatory for Sitka, Alaska (U.S. Naval Observatory 2003).

Analytical Methods

The depth frequencies of tag detections were compared among individual fish and combined to assess group-level depth distributions of sablefish in SJBB. Analyses of tagged fish were performed for the period 5 October 2003 to 14 November 2003, which excluded the initial acclimation period after release (1-4 Oct 2003). Depth detections were corrected for tidal fluctuations by subtracting depth anomalies obtained from a transmitter attached to the receiver buoy. Depth detections for every tagged fish were assigned to one of four diel periods: dawn (nautical dawn to sunrise), day (sunrise to sunset), dusk (sunset to nautical dusk), or night (nautical dusk to nautical dawn; e.g., Beaudreau & Essington 2011). Each detection was also assigned a tide stage of slack (2 hours surrounding the transition between high and low tide), ebb (time from slack associated with high tide to slack associated with low tide) or flood (time from slack associated with low tide to slack associated with high tide). High tides ranged from 6.9 ft to 12.8 ft and low tides ranged from -2.7 to 5.7 ft.

To capture vertical movement, detections were grouped into 10 minute increments to reduce autocorrelation and the increment was assigned a 1 if one or more detections within the increment were ≥5 meters shallower than the mean depth over the increment and a 0 otherwise (Nichol and Somerton, 2002). On rare occasions, a single excursion may have spanned the end of one time increment and the beginning of the following increment, resulting in both increments being classified as excursions for the analysis. Relationships between excursion frequency and environmental variables (diel period and tide stage) were evaluated using generalized linear mixed models (GLMMs) with excursion as the binomial response variable. The probability p that

an excursion occurs within a given 10-min interval was estimated across all six fish by modeling the log-odds ratio (logit-transformed probabilities) as a linear function of the predictors. To provide insight into the individual variability in excursions, generalized linear models (GLMs) were also fit to the data for each fish separately to evaluate if the relationship between predicted excursion frequency and environmental variables was consistent across individuals. The full GLMM and GLM (respectively) had the forms:

$$\log(p / (1-p) = \alpha + a_i + \gamma_j + \delta_k + \beta_{jk}$$

$$\log(p_i / (1-p_i) = \alpha_i + \gamma_{ij} + \delta_{ik} + \beta_{ijk} \quad \text{for fish } i$$

where α is the overall mean log-odds ratio, γ_j is a fixed effect for diel period j, δ_k is a fixed effect for tidal stage k, β_{jk} is an interaction between period j and stage k, and a_i is a random effect for the difference in the mean log-odds ratio of fish i from the overall mean, which is assumed to be normally distributed with mean 0 and variance σ_a^2. All parameters for the GLM include subscript i because all parameters are specific to an individual fish. Parameters were estimated by maximum likelihood; the best fit GLMM model was determined based on the Akaike Information Criterion (AIC) and was used to identify influential predictors. Candidate models included the full model, a model without interactions, and a model with only diel period (γ) or only tide stage (δ). The AIC for each candidate model was subtracted from the minimum AIC (among all models) with the best model having ΔAIC = 0, and models with ΔAIC >10 receiving no support (Burnham and Anderson, 2002). Predictors identified in the overall best GLMM were subsequently used in the GLMs fit for each individual.

Results

All 6 fish that remained within range of the receivers spent the majority of time near the bottom but made periodic vertical movements (Figure 2.2). The bottom depths covered by the receivers ranged from 0 m (shoreline within receiver range) up to 27-32 m (range is from low to high tide) with the majority of the area covered being 20-25 m in depth. Across fish, the mean (± SD) depth was 24.1 ± 4.2 m and individual mean depths ranged from 22.8 ± 4.6 m to 25.2 ± 1.9 m (Table 2.1). Tagged fish depth was plotted through time to visualize vertical movement patterns, revealing the occurrence of excursions into shallower depths (Figure 2.3). After aggregating detections into 10 minute time intervals, 6.6% of the time intervals were classified as excursions for all fish combined across the time series. The proportion of detections that were excursions for individual fish ranged from 1% (fish ID 29800) to 9% (fish ID 30500) from 5 October to 14 November 2003 (Figure 2.4). Within the 6-week detection period, qualitatively the highest frequency of excursions across fish occurred 25 October-5 November (Figure 5).

The mean frequency of excursions (proportion of 10-min intervals classified as 1) was evaluated at each tide stage (slack, ebb, and flood) and diel period (dawn, day, dusk, and night) across all six fish combined (Table 2.2). Mean excursion frequencies appeared slightly higher at slack than at ebb and flood stages. Dawn and day appeared to have the highest mean excursion frequencies, with lower frequencies at dusk and at night (Table 2.2). Generalized linear mixed models (GLMMs) were used to further quantify differences in excursion frequency among tide stages and diel periods and assess their statistical significance (Table 2.3). The best model (ΔAIC=0; Burnham and Anderson 2002) included both environmental variables and an interaction between tide stage and diel period, suggesting significant differences in probability of occurrence among diel periods and tidal stages. The significant interaction suggests that

differences among tidal stages differ by time of day (Figure 2.6). The best fit model was used to calculate the mean estimated proportion of excursions for each set of environmental conditions (Figure 2.6). Overall, the predicted proportion of excursions ($\hat{p}$) was highest during the combination of dawn and flood and dawn and slack stages ($\hat{p}$=0.15 and $\hat{p}$=0.09, respectively). Predicted excursion frequency at ebb for all diel periods was consistently low, and predicted excursions tended to be lower at night, flood and slack stages than at other periods (Figure 2.6).

Individual GLMs suggested that the vertical migration behavior was relatively consistent among individual fish. The confidence intervals for each parameter overlapped among individuals, suggesting low individual variation in the relationship between excursions and environmental variables. Based on individual GLMs, the majority of the tagged fish (ID 29700, 29900, 30000, and 30100) showed the highest excursion frequency during slack stages, while the others (ID 29800 and 30500) appeared to undergo more excursions during flood stages. Dawn was a period of more frequent excursions for 4 out of the 6 fish (ID 29700, 29800, 29900 and 30100), while the other two tagged fish (ID 30500 and 30000) showed more vertical activity during dusk. These comparisons among individual fish at different levels of tide stage and diel period were not statistically tested.

Discussion

Acoustic telemetry on 13 tagged age 0+ sablefish revealed a clear affinity for demersal habitat, with average fish depths at or near the bottom within range of the receivers during the majority of the study period. Five of the tagged fish appeared to leave the area in range of the receivers (average 206 m) since their tags were initially detected but subsequently not redetected.

Notably, 6 fish remained in receiver range throughout the sampling period, showing fidelity to the head of the bay, while regularly undergoing vertical migrations. Further exploration of horizontal movement throughout SJBB and the surrounding area can provide insight into the extent of the variation in mobility among sablefish. It is unclear whether fish moved horizontally simultaneous with vertical migrations; however, due to the rapid changes in depth, excursions appear to show movement up into the water column instead of movement along the bottom into shallower areas within receiver range. Excursions were influenced by tide stage and diel period, with a higher excursion frequency at dawn and during slack and flood stages and a lower excursion frequency at night. However, overall differences were moderate, with the estimated mean probability of excursions in a given 10 min interval ranging from 3% to 15%. There was individual variability in whether the fish stayed within the receiver range and some variability in excursion frequency among the 6 fish that stayed within the head of the bay. In order to better understand the extent of individual variability, it would be useful to monitor more fish by placing receivers throughout the entire bay. Individual variability in movement has been found in other fish, including lingcod (Beaudreau & Essington 2011), largemouth bass, yellow perch, pumpkinseeds, and bluegills (Fish & Savitz 1983), and may be related to foraging and social structure. It is unclear how the variation in frequency and timing of excursions by tagged juvenile sablefish is related to their foraging behaviors.

The depth distribution of tagged juvenile sablefish provides insight into their potential strategies for foraging and predator avoidance at an important life stage within the nearshore environment in southeast Alaska. Based on this study and previous life history information, late young-of-year sablefish may transition away from the neuston to the benthos (Sigler et al. 2001). Furthermore, at smaller body sizes, fish are more vulnerable to predation and many juvenile fish

take refuge on the bottom to reduce exposure, which can limit foraging opportunities (Werner et al. 1983, Valdimarsson et al. 2000). Within SJBB, sablefish may be taking advantage of the substrate for protection; however sablefish may not be sacrificing feeding opportunities while spending the majority of their time on the bottom. There is evidence that sablefish are foraging at or near the bottom, as their diet within SJBB includes benthic prey such as worms, clams, and amphipods and demersal fish such as sculpin (Chapter 1).

Vertical movements in relation to diel and tidal stages have been documented for other demersal fishes in the Pacific Ocean such as blue rockfish, *Sebastes mystinus* (Green et al. 2014), lingcod, *Ophiodon elongatus* (Beaudreau & Essington 2011), and Atka mackerel, *Pleurogrammus monopterygius* (Nichol & Somerton 2002). Vertical migrations are often thought to be associated with foraging behavior (Eggers 1978, Beaudreau & Essington 2011, Green et al. 2014); however, resolving the mechanisms underlying fish movement patterns is difficult. Sablefish consume forage fish, such as Pacific herring and smelts, as well as pelagic invertebrates, such as krill (Chapter 1). The current study found a slightly decreased likelihood of excursions by tagged fish during night, which may be due to reduced foraging behavior by visual predators during periods of low light availability (Eggers 1978). Overall, sablefish underwent excursions during all diel periods and tide stages, suggesting that there are other potential drivers for excursions, such as prey availability and presence of predators. Characterizing the predator and prey fields within SJBB would provide further insight into the link between sablefish movement and foraging decisions.

Within SJBB the tidal exchange reached up to 5 m between low and high tide based on buoy measurements and tidal predictions, and flood and subsequent slack stages may create an influx of pelagic resources (Aubry & Acri 2004), potentially explaining the more frequent

vertical movement of juvenile sablefish found during these tidal stages. The reason for the period of increased frequency of excursions by juvenile sablefish in late October 2003 (Figure 2.5) is unknown, but this time coincided with spring tides which may have provided an influx of allochthonous resources to the bay. Predation on forage fish during flood tide has been favored by predators such as harbor seals (Zamon 2001) and some juvenile fish are hypothesized to conserve energy by moving with a flood tide and remaining near the bottom during ebb tides (Boehlert & Mundy 1988). This study reveals the need for further research on the mechanisms driving fine-scale movements of juvenile sablefish within nearshore habitats. In addition to time of day and tidal stage, there are many other environmental and ecological factors that could play a role in vertical migrations of juvenile sablefish, including temperature, salinity, current speed, and the spatial and temporal availability of prey resources.

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Figures

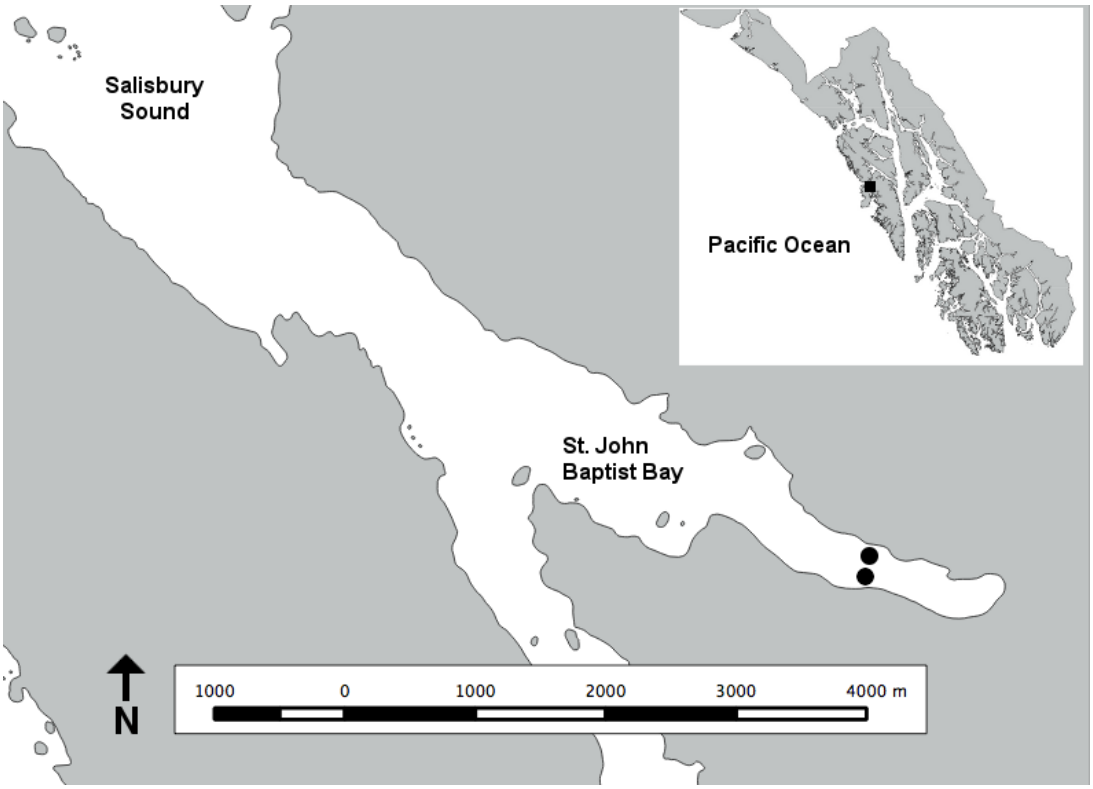

Figure 2.1 Map of study area, St. John Baptist Bay (SJBB), Baranof Island, Alaska. Gray shaded areas represent land and black circles represent the locations of acoustic receivers at the head of SJBB. The inset map in the top right depicts Southeast Alaska with a black square representing the location of the study area.

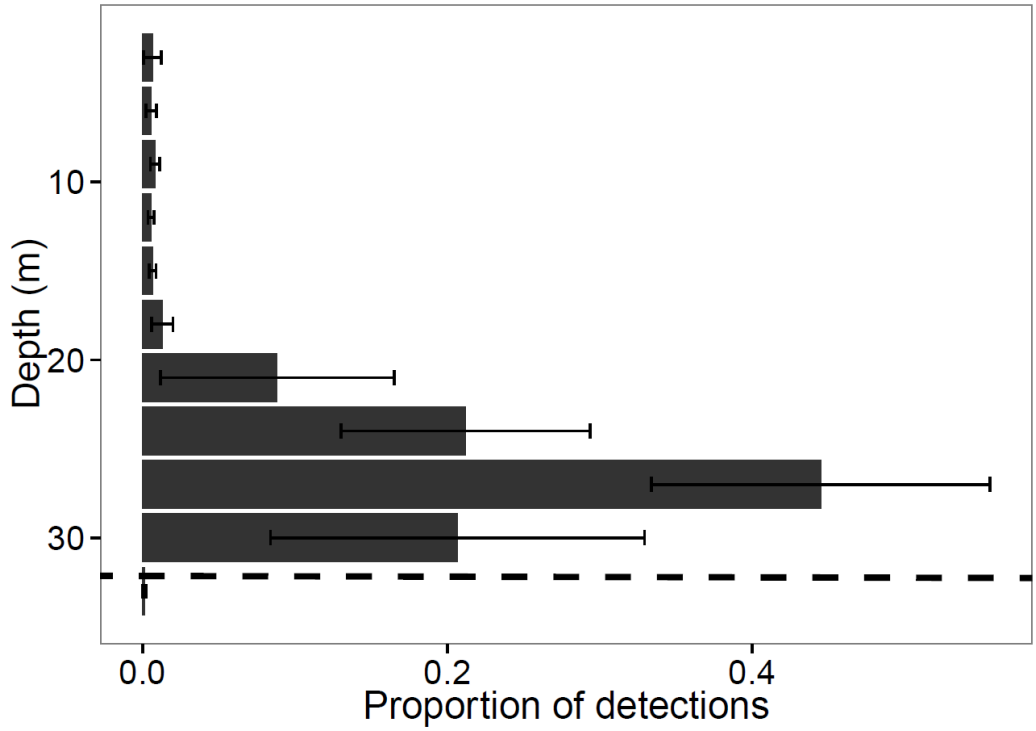

Figure 2.2 Mean proportion of detections across fish (n=6) at 3 m depth increments. Whiskers show ± 2 standard errors. Dashed line represents deepest bottom depth within receiver range (32 m).

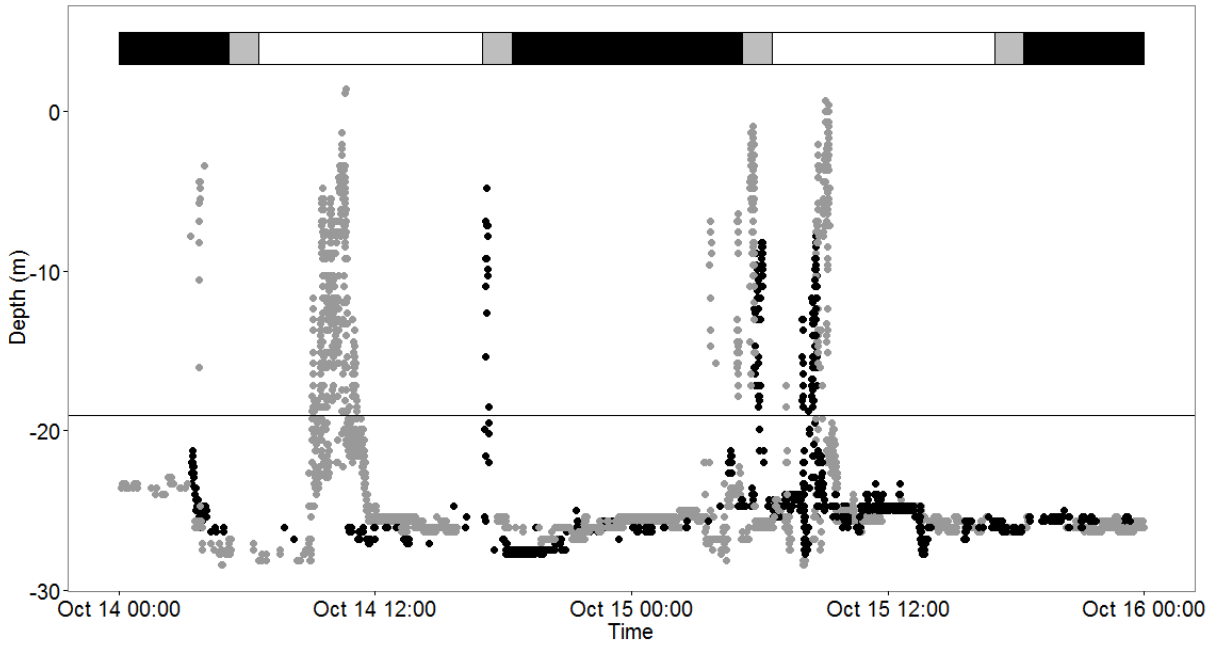

Figure 2.3 Depth distribution over time (48 hours) for tagged fish 29700 (gray dotted line) and 30000 (black dotted line). Horizontal bar above plotted time series represents diel period (black=night, grey=dawn or dusk, white=day). Excursions were defined as shallower than the cutoff depth depicted by the black horizontal line (cutoff=19 m).

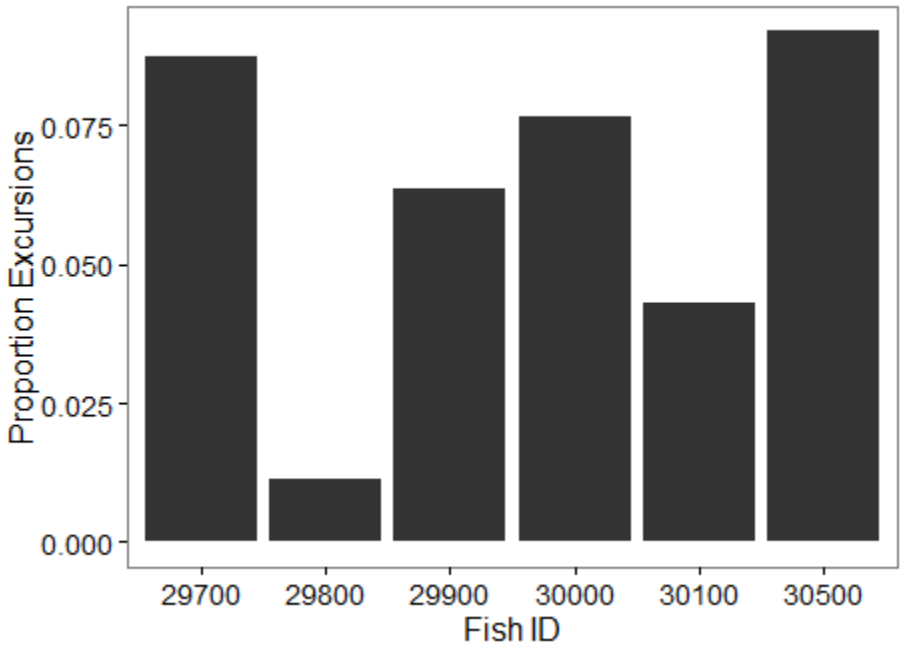

Figure 2.4 Vertical bars represent the proportion of excursions into shallower water for individual fish from 5 October-14 November 2003.

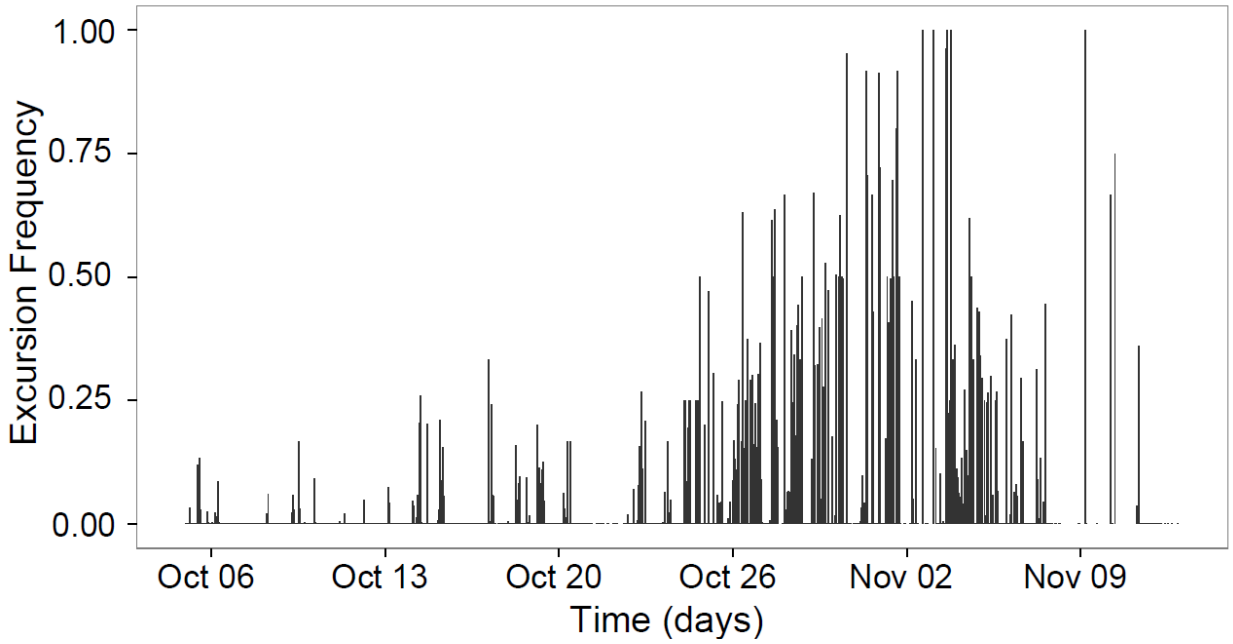

Figure 2.5 Time series of mean excursion frequency across 6 tagged fish in 1 hour time bins from 5 October- 14 November 2003.

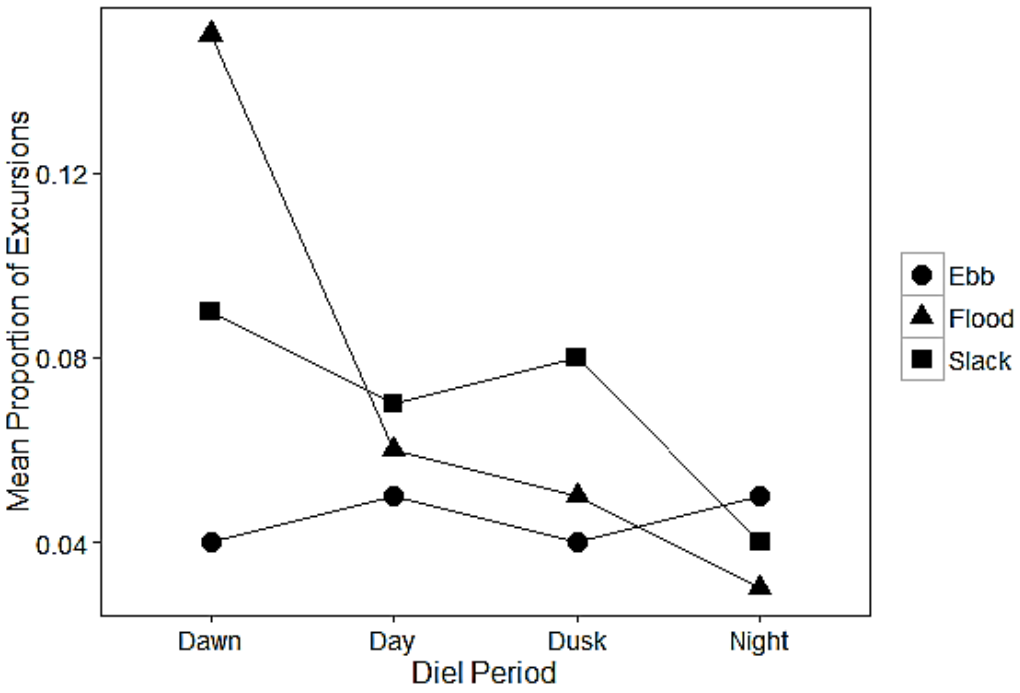

Figure 2.6 Interaction plot showing mean predicted proportion of excursions ($\hat{p}$) for each combination of diel period and tide stage based on best-fit binomial GLMM. The x-axis depicts the diel periods while the symbols represent the tide stages. The y-axis represents the mean of the response variable of excursions.

Tables

Table 2.1 Summary of tagged fish size (fork length; FL in mm), release date post-surgery, detection period, status, and mean depth. Status was assigned to describe initial fish activity: L=left the receiver detection range, R=remained in detection range and M=suspected mortality due to lack of movement (tag release date, FL, and status information from Courtney & Rutecki, 2011). Mean depth was only calculated for fish that remained in detection range (status=R).

Fish ID	Tag Release Date	FL (mm)	Detection period (days)	Status	Depth (m), Mean (±SD)
29500	1 Oct. 2003	245	1	L	
29700	2 Oct. 2003	260	41	R	23.7 (3.9)
29800	1 Oct. 2003	245	35	R	25.2 (1.9)
29900	1 Oct. 2003	240	40	R	24.5 (3.0)
30000	1 Oct. 2003	230	33	R	24.8 (5.7)
30100	1 Oct. 2003	250	38	R	23.4 (4.0)
30200	1 Oct. 2003	240	5	L	
30300	1 Oct. 2003	245	2	L	
30500	1 Oct. 2003	230	35	R	22.8 (4.6)
30600	1 Oct. 2003	225	27	M	
30700	1 Oct. 2003	240	1	L	
30800	2 Oct. 2003	245	12	L	
30900	2 Oct. 2003	250	7	M	

Table 2.2 Mean excursion frequency of all fish (proportion±2 SE) at each tide stage and diel period.

Environmental condition	**Excursion Frequency**
Diel Period	
Dawn	0.09±0.05
Day	0.07±0.03
Dusk	0.05±0.05
Night	0.05±0.02
Tide Stage	
Ebb	0.06±0.03
Flood	0.06±0.03
Slack	0.07±0.03

Table 2.3 Generalized mixed effects models predicting probability of an excursion for 10 minute time intervals with predictors diel period ('Diel'), tide stage ('Tide'), and their interaction term. All possible combinations of fixed effects were considered, with a random effect for the difference in the mean log-odds ratio of individual fish from the overall mean. Differences in the Akaike Information Criterion (ΔAIC) between each model and the best model were calculated.

Model	**ΔAIC**	**A**	**γ_{day}**	**γ_{dusk}**	**γ_{night}**	**δ_{flood}**	**δ_{slack}**
Diel +Tide +Diel:Tide	0	-3.057	N/A (see Figure 5)				
Tide + Diel	12	-2.499	-0.289	-0.521	-0.707	0.028	0.166
Tide	40	-2.962				0.043	0.181
Diel	11	-2.437	-0.281	-0.539	-0.703		
Intercept	40	-2.886					

General Conclusions

Based on the findings of Chapter One, juvenile sablefish in St. John Baptist Bay tend to be generalist predators, consuming 45 benthic, pelagic, invertebrate, and vertebrate prey taxa (taxonomic level varied) during summer and fall sampling periods (July and September, 2012-2013). Pacific herring were the most important prey in terms of weight and occurrence in the diet and were present in all sampling periods where diet was analyzed. Multivariate analyses revealed that diets of juvenile sablefish differed significantly between seasons and years (ANOSIM; Global R=0.278, p<0.001). Diet in summer 2012 was made up of more low-weight, low-energy prey such as larval crabs and barnacle exoskeletons compared to other sample periods. In contrast, in summer 2013, 82% of the diet was Pacific herring. Diet in fall 2012 contained large quantities of krill, while in fall 2013, krill were absent in the diet. In both fall sampling years, pink salmon carcasses were observed within the bay and juvenile sablefish revealed their opportunistic nature by scavenging large quantities of post-spawn salmon skin, organs, eggs and bones, referred to as 'salmonid offal.' In fall 2013, 55% of sablefish diet by weight was salmonid offal, while in fall 2012 salmonid offal made up 13% of the diet by weight. The energetic quality of the diet was highest in September 2013, predominantly due to the large quantities of energy-dense salmonid offal consumed during this period. The seasonal variation in juvenile sablefish diets suggests that they are taking advantage of resources occurring in pulses, such as Pacific salmon, Pacific herring, and krill, while also benefitting from *in situ* prey such as benthic invertebrates that are probably present more regularly.

This new understanding of the temporally variable diet of juvenile sablefish raises further questions. For example, it is evident that Pacific herring are an important resource for juvenile

sablefish in St. John Baptist Bay, but it is unclear how reliant sablefish are on this one prey species. Furthermore, the resource pulse created by salmon migrations in Southeast Alaska provide an energy-rich food source for juvenile sablefish during the fall but it is not known how this resource contributes to their growth and lipid storage for overwinter use. Sablefish, Pacific herring, and Pacific salmon all support valuable commercial fisheries in Southeast Alaska, and understanding how these species interact within a food web can aid in understanding the consequences of their population fluctuations on fisheries. The diversity in juvenile sablefish diets suggest that sablefish may be resilient to fluctuations in Pacific herring or salmon populations because they may have the ability to use a variety of *in situ* resources when herring and salmon are sparse. Further research linking sablefish diet to growth through the use of bioenergetics modeling would help elucidate the importance of high energy pulsed prey resources for juvenile sablefish.

It is apparent that sablefish are using SJBB during multiple seasons and years, and Chapter Two explored the fine scale vertical movement of sablefish in this nearshore habitat. To assess vertical movement, 13 age-0 sablefish were tagged with acoustic transmitters, and two hydrophone buoys with receivers were anchored at the head of the bay from 1 Oct-14 Nov (bottom depth covered 0-32 m). Six tagged fish remained in range of the receivers and these fish were used for discerning patterns in vertical movement. The mean depth of these six fish combined throughout the detection period was 24.1 m. Temporal depth patterns for each fish showed the majority of time was spent on or near the bottom; however, fish underwent excursions into shallower water for short periods of time (usually <10 min). The tagged sablefish spent the majority of their time away from the surface suggesting that by late fall, age-0 sablefish within SJBB are not neuston-oriented, unlike the age-0 sablefish caught earlier in the year in

continental shelf waters (Sigler et al. 2001). The GLMMs used to elucidate the relationship between excursion frequency and diel period and tide stage revealed that excursions were most likely to occur at dawn during flood events and at dawn during slack events. These excursions may be driven by foraging; for example, pursuit of pelagic prey in the water column may occur more often during crepuscular periods. A higher frequency of excursions during flood and slack events may be due to the potential for higher prey activity within the head of SJBB during these tide stages (Aubry & Acri 2004).

Age 0-2 sablefish grow rapidly and inhabit shallow waters on the continental shelf before recruitment into the fishery in the Gulf of Alaska (Cailliet et al. 1988, Rutecki & Varosi 1997, Sigler et al. 2001). The consistent occurrence and residency of juvenile sablefish in SJBB compared to others in the surrounding area suggests this bay is an important and potentially unique rearing habitat for sablefish. Identifying bays with similar characteristics to SJBB may be useful for locating other dense aggregations of juvenile sablefish. SJBB is a muddy, shallow and protected bay, accessible from the Gulf of Alaska due to its outer coast location. The bay has freshwater input and this research suggests that it may be valuable for juvenile sablefish to inhabit coastal marine areas near salmon-bearing streams. There is also potential for sablefish to be entrained into the bay as larvae, which may be elucidated through larval sampling methods. A better understanding of local oceanographic conditions and bathymetry in SJBB would complement ecological information from the current study and further explain why sablefish are reliably found in this bay. In addition, measuring juvenile sablefish consumption rates, growth, and condition in relation to resources used in SJBB would offer a more complete perspective of the importance of key prey items to growth and survival (e.g., Beaudreau & Essington 2009). Moreover, studying the diets of other species found within SJBB to identify potential predators

and competitors may provide more insight into trophic relationships that may affect sablefish survival. The current study contributes 1) vertical movement information, providing a step towards understanding juvenile sablefish strategies for feeding and survival and 2) diet information that is useful for application to multispecies and ecosystem models (Christensen & Pauly 1992, Hollowed et al. 2000, Latour et al. 2003).

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